Lecture 12. Evolution of echolocation

Evolution of echolocation

- Echolocation basics
- Evidence for how and when it appeared
- Continuing evolution of echolocation

- Send out a pulse of sound; receive echoes
  - Orientation
  - Navigation
  - Communication
  - Hunting

Sound production

- Sound produced by the larynx (laryngeal echolocation)
- Emitted either through the nose or through the mouth
- Correlate calls with wing flaps to increase pressure in larynx
- Lots of neurological modifications
- Ultrasonic (to humans): 20 – 100 KHz

- Limitations
  - Can't pulse and breathe
  - Sound attenuates in air—have to be pretty close to your target
  - Don't want to deafen yourself—up to 120 decibels
Perceptual problems

- Detection—what's there?
- Classification—what is it? how big is it? is it edible?
- Localization—where is it? how far away is it? is it moving?

Detection:
- Separating prey from background

Classification:
- Size
- Shape
- Material
- Texture

Localization:
- Distance—time delay of echo
- Horizontal (azimuthal) angle—binaural cues
- Vertical angle (elevation)—monaural spectral cues
- Motion—Doppler shifts, "glints"
Lecture 12. Evolution of echolocation

Additional perceptual problems

- Environmental noise
- “Clutter” echoes
  - Other prey
  - Stationary objects and non-prey
  - Ground, vegetation
- Other bats’ signals

Tradeoffs

- Narrowband (CF)
  - Constant frequency (CF)
  - Change only a few hundred Hz
  - Quasi-constant frequency (QCF) or shallow modulation
  - Change a few kilohertz (kHz)
- Broadband
  - Frequency modulation (FM) or steep modulation
  - Harmonics (multiples of a fundamental frequency)—use more frequencies to scan more broadly

Tradeoffs

- Narrowband (CF)
  - Detect weak echoes but can’t localize well (bad for time), especially with long pulses
  - Doppler compensation and frequency shifts allow detection of motion and fluttering (“glints”)
  - Temporal overlap is ok since echoes are frequency-shifted
- Broadband (FM)
  - Harder to detect echoes, but better for accurate determination of distance and angles as well as characterization
Lecture 12. Evolution of echolocation

Call structure varies among bats, among habitats, among prey, and within a call sequence

Schnitzler et al., TREE 2003

Bats are not alone...

- Swiftlets (Aerodramus) & oilbird (Steatornis)
- In mammals:
  - Most bats
  - Toothed whales & dolphins
  - Some shrews
  - Some tenrecs

How many times?

"Besides bats, dolphins also use echolocation. According to evolution, similar animals descended from each other, so if evolution is true, bats descended from dolphins or vice versa."

Not all echolocation is the same
Whales, bats, shrews, and tenrecs are distant relatives (four different orders)

Echolocation (of some sort) has evolved independently at least four times in mammals.

Laryngeal echolocation in bats is much more sophisticated.
Lecture 12. Evolution of echolocation

- Microbats echolocate
- One genus (*Rousettus*) of megabats echolocates

...but (again) not all echolocation is the same

*Rousettus* uses tongue-clicks (similar to birds)
This is (probably) different in evolutionary terms than sophisticated laryngeal echolocation

Traditional (morphological) view of bat phylogeny:
Lecture 12. Evolution of echolocation

Teeling et al. 2005

Monophyletic Megachiroptera
Paraphyletic Microchiroptera!

2 changes total
Lecture 12. Evolution of echolocation

Icaronycteris index (Green River, Wyoming, 50 Mya)

Hassianycteris—radiograph
Lecture 12. Evolution of echolocation

Did the fossils echolocate?

- Moderately expanded cochlea
- Stylohyal (of hyoid) expanded cranially at the tip
- Large orbicular process on the malleus

These characters are associated with echolocation in extant bats

- Electron microscopy shows pollen on wingscales of eaten moths

Yes, the Eocene bats already used echolocation!

Teeling et al. 2005 & Springer et al. 2001
Lecture 12. Evolution of echolocation

- Eocene bats flew AND echolocated!

  - Three hypotheses:
    - Flight first—echolocation may have started off as orientation/navigation
    - Echolocation first—flight later to reduce competition with other terrestrial small mammals
    - Tandem evolution—two major innovations evolved together

- No transitional forms (“missing links”) between ancestors and bats
  - Fossils with wings but no echolocation?
  - Fossils that echolocated but couldn’t fly?
Lecture 12. Evolution of echolocation

[Graph showing correlation between echolocation width and basilar width for various species of bats]

[Graph showing inter-nasal index and brachial index for extinct and extant bats]

[Phylogenetic tree showing relationships between different bat species and outgroups]
“Forelimb anatomy indicates that the new bat was capable of powered flight like other Eocene bats, but ear morphology suggests that it lacked their echolocation abilities, supporting a ‘flight first’ hypothesis for chiropteran evolution. The shape of the wings suggests that an undulating gliding–fluttering flight style may be primitive for bats, and the presence of a long calcar indicates that a broad tail membrane evolved early in Chiroptera, probably functioning as an additional airfoil rather than as a prey-capture device. Limb proportions and retention of claws on all digits indicate that the new bat may have been an agile climber that employed quadrupedal locomotion and under-branch hanging behaviour.”
Insect defenses

- Ears (tympani)
  - 19 separate times—on legs, abdomens, thoraces, wings, facial palps...
  - “Tune” ears to local bat predators (e.g., noctuid Ascalapha odorata) in Hawaii
- “Jamming” ultrasound?
- “Stealth” scales
- Unpalatable and obvious (aposematic signaling)
- Tiger moths
- Flight behavior—fly close to ground, dive, steer away
- Sit still and look like background
- Predator swamping
  - Midge, other swimmers
- …many many more that we don’t know about—morphological, physiological, behavioral…

Bat responses

- “lowball” or “highball” frequency to be inaudible to prey
- Lower volume—whispering bats
- Use prey cues with (or instead of) echolocation
- Exploit insect behavior
  - Eating an insect that is avoiding another bat doubles success rate
- Sneak up via vegetation, or sit still
- Eat something that can’t hear you—birds, frogs
- Vary strategy depending on particular prey
- Trick prey by changing pulse as you get closer to make yourself sound farther away
- Develop ways to overcome stealth scales and jamming ultrasound

Evolution by echolocation

- “Harmonic-hopping” frequency changes driving divergence (Kingston & Rossiter 2004, Nature)
- Harmonics affect bat’s perception of distribution of prey (size, type, etc)